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A pictorial representation of peristomal architecture

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Abstract

The terminology associated with the use of peristomes in the identification and classification of mosses is cumbersome and difficult to understand. This paper provides a pictorial explanation of peristomal architecture with its associated terminology, such as nematodontous and arthrodontous peristomes, and the division of the latter into diplolepideous and haplolepideous peristomes. (*The Victorian Naturalist* **123** (4), 2006, 203-211)

The moss plant normally seen and recognised is referred to as a gametophyte as it produces the gametes, i.e. egg and sperm. When the sperm fertilizes the egg a sporophyte develops. The sporophyte is ephemeral and essentially remains dependent on its gametophyte parent (Fig. 1), i.e. nutrients are obtained from the gametophyte parent through the basal foot of a stalk-like structure (the seta) that remains embedded within the parental gametophyte tissue. A spore capsule terminates this seta (Fig. 1).

Many mosses have one or more rings of teeth around the mouth of the capsule (Fig. 2). The teeth collectively are referred to as the peristome (Fig. 1) and are protected by an operculum or lid (Fig. 1), which falls off when the spores are mature. However, not all mosses have peristomes.

The outer ring of teeth (exostome) in double peristomes (Fig. 2) may exhibit hygroscopic movement in response to changes in humidity by bending backwards and forwards (Proctor 1984). The movement provides a gentle catapulting action for launching spores a short distance into the air, where they may be caught by a gentle breeze and dispersed to an environment suitable for germination. Subsequent to germination, spores will develop into another gametophyte generation. Hygroscopic movement of the exostome may be particularly relevant in closed forest situations where opportunities for air transport of spores needs to be maximized. The inner ring of teeth (endostome) (Fig. 2) may regulate spore dispersal by gradually sifting the spores.

As spore dispersal mechanisms in mosses, peristomes are specialised, intricate and architecturally elaborate. Adaptive trends of morphological characters have resulted

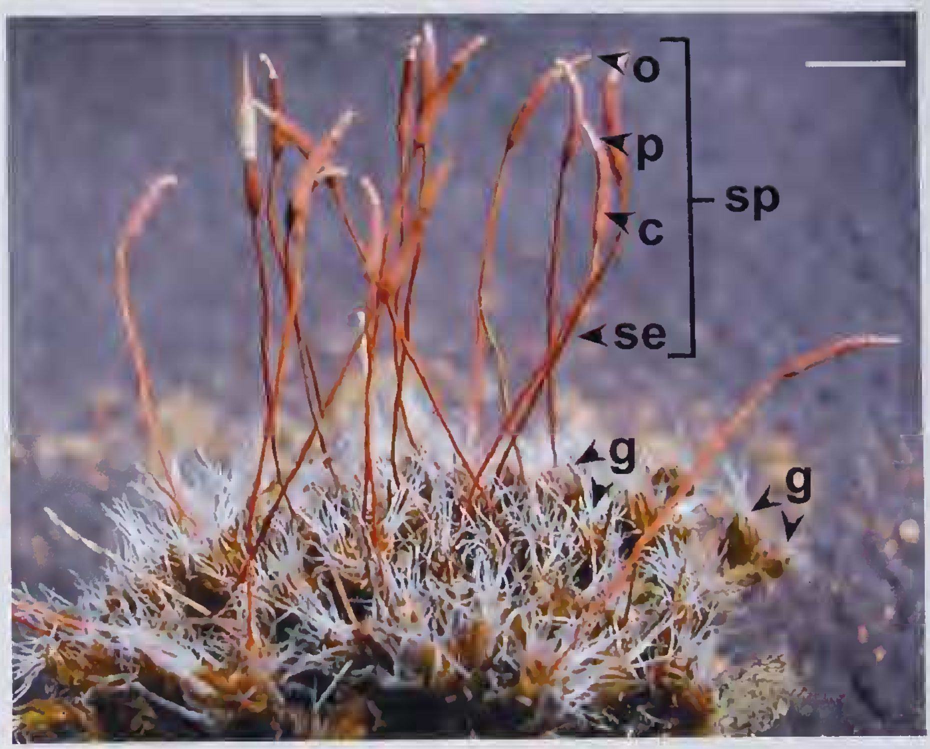

Fig. 1. Colony of *Tortula antarctica* (Hampe) Wilson. Leafy gametophyte (g) with dependent sporophyte (sp) bearing a mature capsule (c) terminating a seta (se). A peristome (p) of long teeth occurs at the mouth of the capsule. This peristome initially is covered by an operculum (o) which is shed when spores become mature. Scale bar is 3.5 mm.

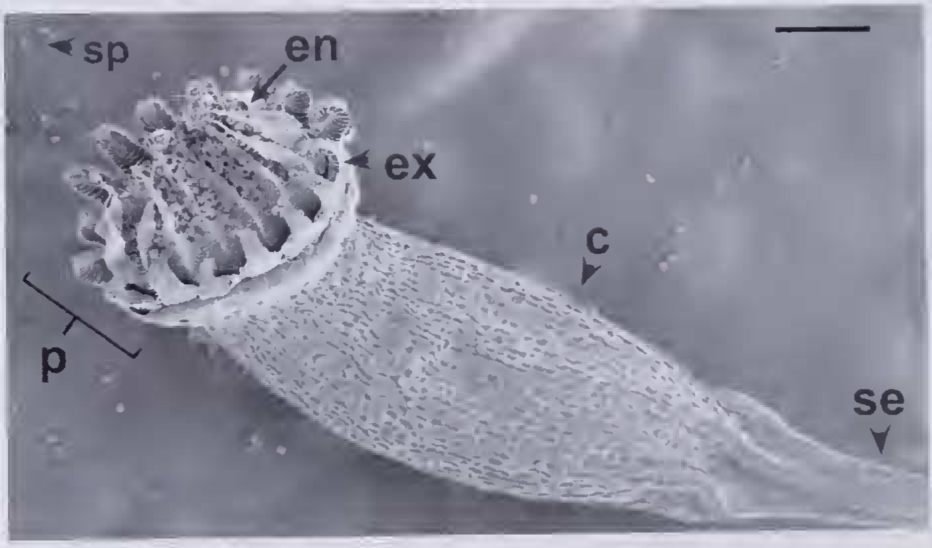

Fig. 2.. Capsule (c) of *Hypnum cupressiforme* Hedw. with peristome (p) showing an outer row of teeth, the exostome (ex), and an inner row of teeth, the endostome (en). Spores (sp). Scale bar is 200 µm.

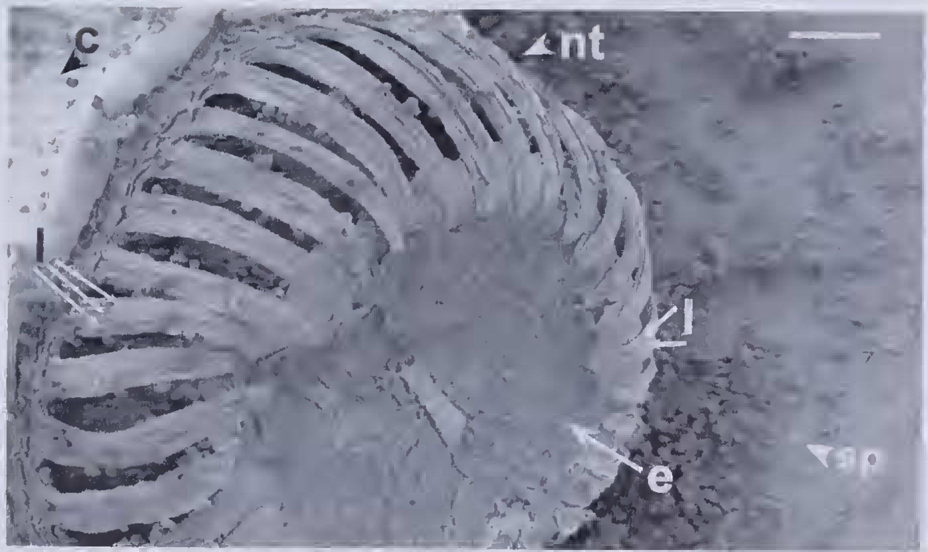

Fig. 3.. Nematodontous teeth (nt) of *Atrichum androgynum* (Müll. Hal.) A. Jaeger. Teeth are made up of layers (l) of whole cells. Tips of teeth attach to the disc-like epiphragm (e). Slight air movement causes release of spores between the teeth. Capsule (c). Spores (sp). Scale bar is 100 µm.

in different peristomal configurations that have been used as important tools in higher level classification of mosses for over 150 years (Vitt 1999). Three peristomal characters are vital to classification. These are cell structure of the teeth, the arrangement of the outer teeth relative to the inner teeth (where present), i.e. whether the outer teeth are alternate or opposite the inner teeth, and the initial cell alignment (Goffinet *et al.* 1999).

In the first instance, peristomes are divided into two types, nematodontous and arthrodontous peristomes. In terms of peristomal architecture, this division is as important as the division between monocotyledons and dicotyledons in flowering plants, although the distinction is at a lower classificatory level for the mosses than for the flowering plants.

Nematodontous peristomes have teeth composed of whole, dead and 'mostly elongate cells in one or more layers' (Crum 2001) with walls thickened uniformly (Shaw *et al.* 1989). However, arrangement of the cells can vary from species to species. Figure 3 details layers of whole cells which occur in nematodontous teeth. In the species depicted, *Atrichum androgynum* (Müll. Hal.) A. Jaeger, the tips of the teeth are attached to a disc-like epiphragm that releases spores with the help of a little air movement. In essence, spores are released via a pepper shaker effect. *Dawsonia superba* Grev. var. *pulchra* (Fig. 4) shows another method of spore dispersal where the nematodontous teeth take the form of multicellular filaments forming a twirled 'brush'. When the spores mature, the 'brush' untwists, allowing gradual release of the spores.

Arthrodontous peristomes have teeth composed of thickened cell wall remnants of squat cells occurring in two or three cell layers (Crum 2001) involving the outer, primary and inner peristome layers, i.e. OPL, PPL, and IPL respectively. This means that during development of the teeth, cell wall plates located parallel to the capsule rim (periclinal), become differentially thickened, while much of the cross-wall and radially vertical cell wall material perpendicular to the capsule rim (anticlinal) becomes reabsorbed (Buck and Goffinet 2000). Ninety percent of true mosses are classified as arthrodontous (Crum 2001).

Arthrodontous peristomes are further divided into diplolepideous and haplolepideous peristomes. Diplolepideous peristomes usually have a double layer of teeth,

Fig. 4. The brush-like nematodontous teeth (nt) of *Dawsonia superba* Grev. var. *pulchra* Zanten facilitates spore release as it untwists. Capsule (c). Spores (sp). Scale bar is 50 µm.

the exostome forming the outer teeth and the endostome forming the inner teeth. It is the outer row that is of vital importance to classification, principally because the inner row of teeth may be reduced to nothing more than a fragile collar-like basal membrane (Fig. 5). However, more typically the endostome consists of this basal membrane with 16 teeth (also referred to as segments) which are keeled, perforated and alternate with cilia (in groups of one to four) in many species (Fig. 6) (Magombo 2003).

The exostome generally consists of 16 teeth (Shaw and Renzaglia 2004), which

Fig. 5.. Diplolepideous peristome of *Glypothecium sciuroides* (Hook.) Hampe showing 16 outer teeth constituting the exostome (ex). The exostome is vitally important to classification as the inner teeth or endostome (en) may be reduced to a collar-like basal membrane, as depicted in this figure. Capsule (c). Spores (sp). Scale bar is 50 µm.

Fig. 6.. Elaborate diplolepideous peristome of *Ptychomnion aciculare* (Brid.) Mitt. showing exostome (ex) of 16 teeth, and endostome (en) of basal membrane with 16 keeled teeth (also known as segments). Perforations occur along the upper section of each keel (k) and two cilia (ci) alternate with each segment. An endostome showing a basal membrane with teeth is more typical of a diplolepideous peristome than the reduction of the endostome to just a collar-like basal membrane. Spores (sp). Scale bar is 100 μm.

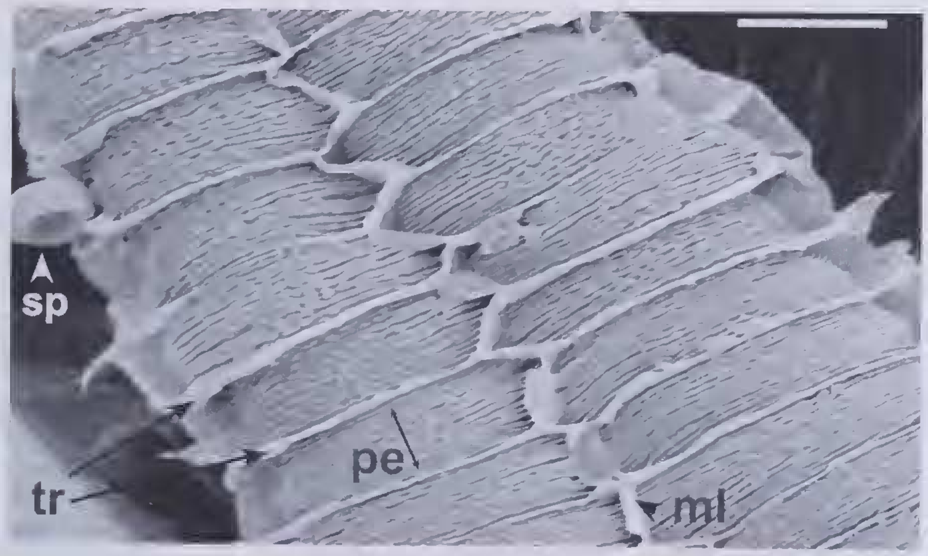

Fig. 7.. Diplolepideous exostome tooth of *Hypnodendron vitiense* Mitt. showing the outer face consisting of two columns of periclinal (parallel to the capsule rim) cell wall plates (pe) of former cells. The trabeculae (tr) derived from cross-walls on the outer face of each exostome tooth and the zig-zag median line (ml) reflect the two columns of cells that form each tooth, i.e. the trabeculae and median line represent anticlinal (perpendicular to the capsule rim) cell wall remnants and border the periclinal cell wall material. The term 'diplolepideous' refers to this twin column formation. Spores (sp). Scale bar is 20 μm.

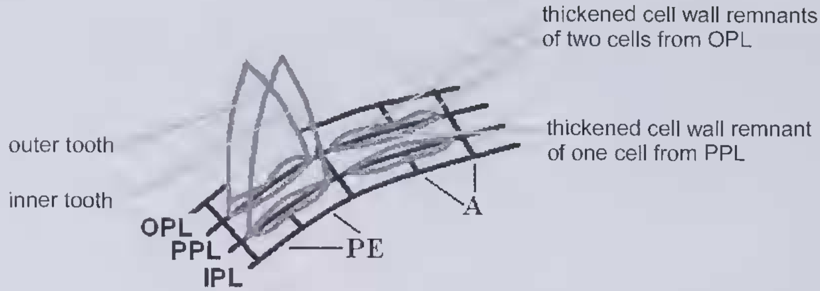

Fig. 8.. Diagram of a diplolepideous peristome (after Buck and Goffinet 2000) showing exostome (outer teeth) and endostome (inner teeth) opposite each other. Much of the anticlinal cell wall material perpendicular to the capsule (A) becomes reabsorbed. Periclinal walls (PE). Outer peristomal layer (OPL). Primary peristomal layer (PPL). Inner peristomal layer (IPL).

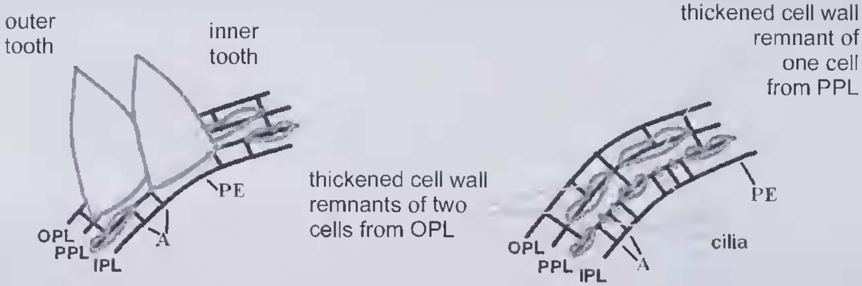

Fig. 9.. Diagram of a diplolepideous peristome (after Buck and Goffinet 2000) showing alternate exostome (outer teeth) and endostome (inner teeth). Much of the anticlinal cell wall material (A) perpendicular to the capsule becomes reabsorbed. Periclinal walls (PE). Outer peristomal layer (OPL). Primary peristomal layer (PPL). Inner peristomal layer (IPL).

have an outer face of two columns and an inner face of a single column (OPL + PPL), each column consisting of a stack of periclinal cell wall plates of former cells. The horizontal lines (trabeculae) derived from cross-walls (Fig. 7) on the outer face of each exostome tooth, and the zig-zag median line, reflect the structure of the two columns of cells occurring side by side (Edwards 1984; Shaw *et al.* 1989). The term diplolepideous refers to this twin column formula (Fig. 7).

Diplolepideous peristomes may be configured with an 'opposite' peristome cell pattern (Fig. 8) or an 'alternate' peristome cell pattern (Fig. 9), i.e. with the exostome and endostome teeth opposite or alternate to each other respectively. Figure 10 shows the exostome teeth opposite endostome teeth while Fig. 11 shows *Hypnum cupressiforme* Hedw., with exostome teeth alternating with endostome teeth. From an evolutionary point of view, the 'opposite' arrangement of the endostome and exostome is considered more primitive (Vitt 1984).

Haplolepideous peristomes have teeth with an outer face of one column consisting of wall remnants of a stack of cells and an inner face of two columns (PPL + IPL) consisting of wall remnants of two stacks of cells. Haplolepideous peristomes usually consist of a single layer of 16 teeth (Shaw and Renzaglia 2004). The term haplolepideous refers to the outer face consisting of wall remnants of the single stack of cells. The horizontal lines (trabeculae) (Fig. 12) correspond to the top and bottom plates. Figure 13 represents the haplolepideous configuration. It is thought that the haplolepideous peristome (Fig. 14) is

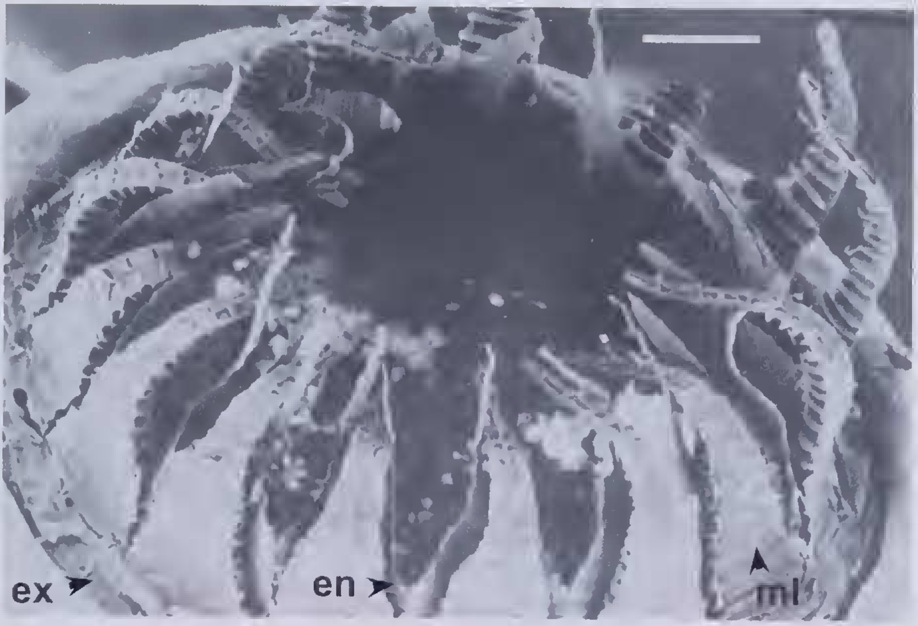

Fig. 10.. Funaria-type diplolepideous peristome showing 'opposite' tooth arrangement. Exostome of outer teeth (ex). Endostome of inner teeth (en). Zig-zag median line (ml). In evolutionary terms, the 'opposite' arrangement of outer and inner teeth is considered more primitive than the alternate tooth arrangement shown in Fig. 11. Scale bar is 40 μm.

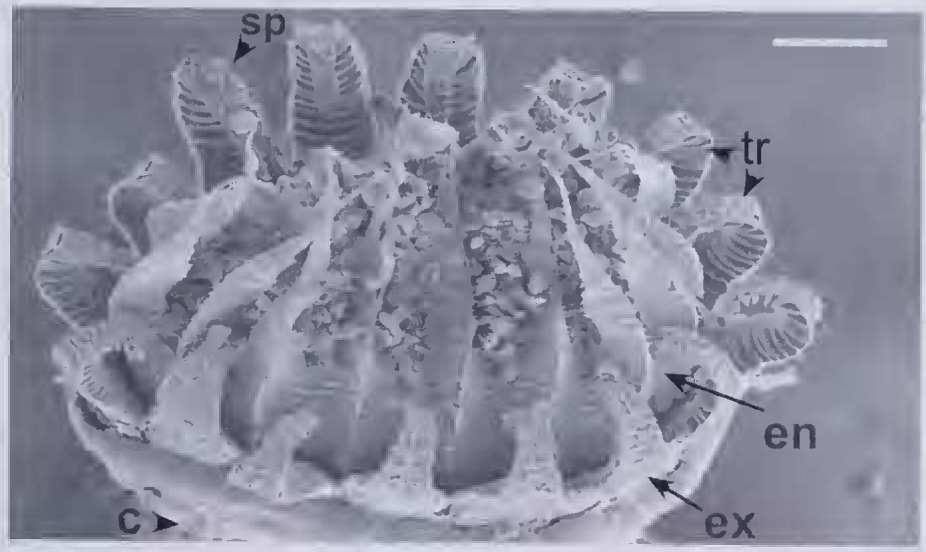

Fig. 11.. Diplolepideous peristome of *Hypnum cupressiforme* Hedw., showing 'alternate' tooth arrangement. Exostome of outer teeth (ex). Endostome of inner teeth (en) with basal membrane and keeled, perforated teeth (segments). Cilia alternate with segments, but are obscured by spore mass. Exostome teeth are trabeculate (tr) on both the outer face and inner face but the inner face is deeply trabeculate. Capsule (c). Spores (sp). Scale bar is 100 μm.

Fig. 12.. Outer face of haplolepideous teeth of *Dicranoloma menziesii* (Taylor) Renauld showing trabeculae (t) reflecting the wall material of a single column or stack of cells that forms each tooth, contrasting with the two columns of diplolepideous teeth shown in Fig. 7. The trabeculae correspond to the top and bottom cell wall plates which are anticlinal, i.e. perpendicular to the capsule rim. The material seen between the trabeculae is the periclinal cell wall remnants, i.e. cell wall remnants parallel to the capsule rim. Scale bar is 10 µm.

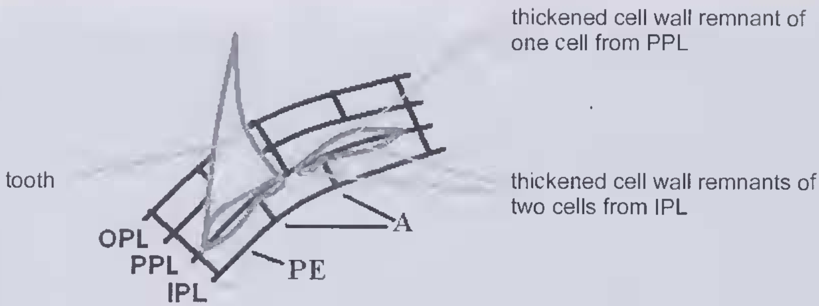

Fig. 13.. Diagram of haplolepideous peristome (after Buck and Goffinet 2000). Much of the anticlinal wall material (A) perpendicular to the capsule becomes reabsorbed. Periclinal walls (PE). Outer peristomal layer (OPL). Primary peristomal layer (PPL). Inner peristomal layer (IPL).

derived from the diplolepideous peristome with opposite endostome and exostome, and is homologous with endostomal segments (Buck and Goffinet 2000; Magombo 2003; Newton and Cox 2000; Shaw and Renzaglia 2004; Vitt 1981).

Peristomal terminology does not end here, but the above detail provides readers with an introduction to this cumbersome language belonging to the intricate, elaborate and beautiful world of peristomal architecture, moss identification and classification. Study of these ancient plants and their reproductive innovations is crucial to understanding the evolution of land plants (Shaw and Renzaglia 2004).

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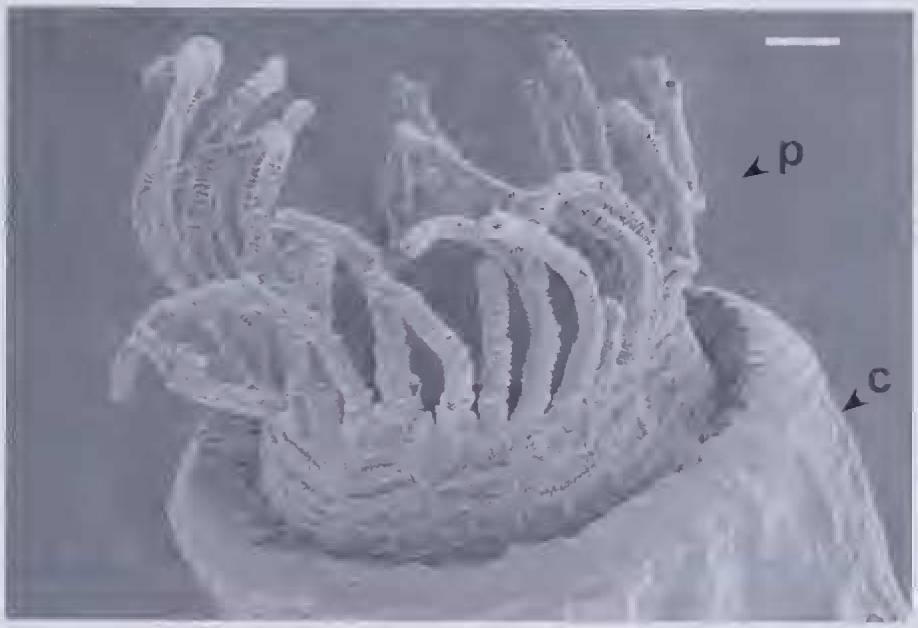

Fig. 14.. *Tortula recurvata* Hook. showing haplolepideous peristome (p) consisting of basal membrane and 32 tubular teeth. Capsule (c). The haplolepideous peristome is believed to be derived from the diplolepideous peristome with opposite exostome and endostome as depicted in Fig. 10, and that it is homologous with endostomal segments. Scale bar is 40 μm.

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